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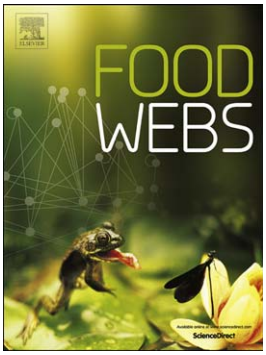

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Stable isotopes reveal insight into food web dynamics of a data-poor deep-sea island slope community

Oliver N. Shipley[1, 2, 3*], Nicholas V. C. Polunin[1], Steven P. Newman[1, 4], Christopher J. Sweeting[1], Sam Barker[5], Matthew J. Witt[5] and Edward J. Brooks[2]

[1]School of Marine Science & Technology, Newcastle University, Newcastle upon Tyne NE1 7RU UK

[2]Shark Research and Conservation Program, Cape Eleuthera Institute, Eleuthera, The Bahamas, PO Box EL-26029

[3]School of Marine and Atmosphere Sciences, Stony Brook University, 11780 NY, USA

[4]Banyan Tree Marine Lab, Vabbinfaru, Kaafu Atoll, Maldives

[5]The Environment and Sustainability Institute, University of Exeter Penryn Campus, Cornwall, TR10 9EZ, UK

**Corresponding author*

Abstract

Deep-sea communities are subject to a growing number of extrinsic pressures, which threatens their structure and function. Here we use carbon and nitrogen stable isotopes to provide new insights into the community structure of a data-poor deep-sea island slope system, the Exuma Sound, The Bahamas. A total of 78 individuals from 16 species were captured between 462 m and 923 m, and exhibited a broad range of $\delta^{13}C$ (9.45‰) and $\delta^{15}N$ (6.94‰). At the individual-level, $\delta^{13}C$ decreased strongly with depth, indicative of shifting production sources, as well as potential shifts in community composition, and species-specific feeding strategies. $\delta^{15}N$ did not follow strong depth relationships, suggesting trophic level and depth are not tightly coupled across individuals. We observed ontogenetic enrichment in $\delta^{13}C$ and $\delta^{15}N$ for *Squalus cubensis* (Cuban dogfish) highlighting a shift to larger, higher trophic level prey through ontogeny. These data provide the first assessment of food-web structure in the Exuma Sound, and suggest inherent complexity associated with deep-sea island slope ecosystems. Such observations are needed to further our understanding and develop contemporary management plans for these systems.

Keywords: Stable isotope analysis; deep-water; ecosystem; primary production; feeding dynamics

1. Introduction

Deep-sea ecosystems are being increasingly exploited by a multitude of anthropogenic activities, such as commercial fishing and mining, which threatens their structure and function (Benn et al., 2010; Priede et al., 2010; Van Dover et al., 2011). The conservative life histories of many deep-sea taxa exacerbate exploitative effects, as many are unable to quickly rebound from population-based perturbations (Simpfendorfer and Kyne, 2009). Such effects are likely to drive changes in community composition, and structure, as seen in a number of coastal biomes (e.g. McCain et al., 2015; Möllman et al., 2015). Therefore a basic understanding of food-web dynamics is essential for predicting the broad-scale impacts of exploitation on deep-sea communities.

Stable isotope analysis (SIA) of carbon and nitrogen (referred to in delta notation as $\delta^{13}C$ and $\delta^{15}N$) has proven valuable in describing food-web structure and species interactions across marine, freshwater, and terrestrial biomes (Layman et al., 2011; Hussey et al., 2012; Rundel et al., 2012), and are becoming increasingly applied to deep-sea systems (Polunin et al., 2001; Pethybridge et al., 2012; Churchill et al., 2015; Shipley et al., In Press). Although the majority of isotopic food-web studies have focussed on shallow water systems, evidence suggests deep-sea

community structure is highly complex (Portail et al., 2016), can encompass many trophic guilds (Valls et al., 2014), and is often supported by multiple sources of primary production (Newman et al., 2011; Reid et al., 2012). Deep-sea island slope communities are of particular interest to managers, as they occur at the interface between productive neritic and more oligotrophic open-ocean systems. Given their proximity to a multitude of potential energy pools, these systems may exhibit a unique suite of community dynamics and support a highly diverse range of taxa (Suchanek et al., 1985). Despite this, deep-sea island slopes are amongst the most poorly represented across the scientific literature (Shipley et al., *In Press*), highlighting a critical need to further examine these systems.

The Exuma Sound is a deep-water (~1700m max depth) inlet of the Atlantic Ocean, categorised by narrow continental shelves, which drop from 30m to 400m at the shelf-break. The continental slope is categorised by rugose limestone outcroppings creating a complex bathymetry (Ball et al., 1969), which transitions into a featureless sandy benthos at the bottom (Crevello and Schlager, 1980). Data are sparse, but the system appears to support high megafaunal diversity and abundance (Brooks et al., 2015). Here we use carbon and nitrogen stable isotopes to explore the food-web structure of the Exuma Sound deep-sea island slope community. We provide the first reported $\delta^{13}C$ and $\delta^{15}N$ values for a number of species, and explore potential factors responsible for patterns in isotope values across individuals.

2. Methods

Sampling was conducted in the northeast Exuma Sound, off south Eleuthera, The Bahamas (24.54°N, 76.12°W; WGS84), between November 2013 and May 2014, under permits MAF/FIS/17 and MAF/FIS/34 from the Bahamian Department of Marine Resources. Animal sampling followed the requirements of the UK Home Office Scientific Procedures (Animals) Act and Association for the Study of Animal Behaviour (Rollin and Kessel, 1998). Animals were captured using deep-sea longlines (see Brooks et al., 2015 for detailed methods) and square and cylindrical baited fish traps soaked for 24 hours. White muscle tissue, which provides a relatively long-term (weeks to months) indication of diet (Hussey et al., 2012) was excised dorsally for fish and eels, and taken from appendages for invertebrates. Tissue was then stored at -20°C prior to SIA. Tissues were freeze-dried and homogenised prior to polar compound (lipid, urea and trimethylamine N-oxide (TMAO)) extraction with a 2:1 chloroform methanol solution (Sweeting et al., 2006; Churchill et al., 2015). Approximately 0.6 ± 0.1 mg of dried tissue was then weighed into 6x4 mm tin-capsules.

All samples were analysed in duplicate for $\delta^{15}N$, $\delta^{13}C$, %N and %C using a Sercon INTEGRA2 stable isotope mass spectrometer (SerCon Ltd, Cheshire, UK) at the Environment and Sustainability Institute, University of Exeter, Penryn Campus, UK. Values are referred to in δ notation following the equation: $\delta^{b}X[(R_{sample}/R_{standard})-1] \times 1000$ where X^{b} = isotopic element chosen for analysis, R_{sample} = heavy to light isotope ratio derived from the sample, and $R_{standard}$ = heavy to light isotope ratio derived from the standard (DeNiro and Epstein, 1978). Isotope ratio scales were normalised through Vienna Pee Dee Belemnite for carbon, and atmospheric N_2 for nitrogen using IAEA standards of lithium carbonate (LSVEC), CH-6 and N-1, N-2 respectively. To determine analytical precision (standard deviation), two alanine standards were placed between every 8 samples (n = 162, < 0.15 S.D.). Batch precision was determined with an internal reference of blue antimora (*Antirmora rostrata*) white muscle tissue, which was placed at the beginning and end of every run (n = 32, < 0.15 S.D.). A two-point linear correction (Paul et al., 2010) was applied to $\delta^{15}N$ values based on IAEA N-1 and N-2 values. The accuracy of the carbon IAEA reference materials was such that a two point linear correction was not necessary.

At the individual level, Generalized Linear Models (GLM's) were used to determine whether variation in $\delta^{13}C$ and $\delta^{15}N$ was best explained by depth, species, or an interaction between both variables. For *S. cubensis*, body-size relationships with $\delta^{13}C$ and $\delta^{15}N$ were assessed using least-squares regression. All statistical analyses were performed in 'R' (Version 3.0; R development core team, 2007).

3. Results

A total of 78 individuals from 16 species were captured from the northeast Exuma Sound, at depths ranging from 462 m to 923 m (Table 1). At the individual level, community $\delta^{13}C$, $\delta^{15}N$ and C:N ranged from -10.77‰ to -20.22‰, 6.99-13.93‰, and 2.57 to 3.34 respectively (Table 1).

The effect of depth (glm, $t = -4.62$, $p < 0.001$), species ($t = -2.48$, $p < 0.02$), and interaction of the two factors ($t = 2.57$, $p < 0.02$) all proved significant in explaining variation in $\delta^{13}C$, which became more depleted in individuals at greater depths. Variation in $\delta^{15}N$ could not be explained by depth ($t = 0.41$, $p > 0.15$), species ($t = 1.02$, $p > 0.15$), or interaction of both factors ($t = 0.81$, $p > 0.15$). For *Squalus cubensis* $\delta^{13}C$ (least-squares regression, $r^2 = 0.69$, $p < 0.001$) and $\delta^{15}N$ (least-squares regression, $r^2 = 0.26$, $p < 0.001$) both became enriched with increasing size.

Table 1.

Fig 1.

4. Discussion

The wide range of $\delta^{13}C$ (9.45‰) and $\delta^{15}N$ (6.94‰) values across individuals suggests a unique and complex food web structure, spanning a number of trophic levels in which biomass may be underpinned by a mix of potential production sources. At the individual level, $\delta^{13}C$ became more depleted in individuals captured at greater depths. Such patterns could be explained by a number of factors including shifting production sources, or shifts in community composition and thus faunal-specific feeding strategies (i.e. switching from benthic to pelagic prey) (Trueman et al., 2014). The major energy pools supporting deep-sea food-web productivity are poorly defined, aside from oligotrophic open-ocean (phytoplanktonic-POM) and hydrothermal vent (Chemoautotrophic and phytoplanktonic POM) communities. However, a significant proportion of neritic-derived primary production may be transported into deep-sea systems at some locales (Suchanek et al., 1985; Sanchez-Vidal et al., 2012), and if assimilated into the food web, could drive the more enriched $\delta^{13}C$ values found in shallower individuals.

Fig 2.

As the variability in $\delta^{13}C$, was also part explained by species, and the interaction between species and depth, a shift in community composition, could also part-explain the depletion in $\delta^{13}C$ with depth, especially for fishes. *M. canis-insularis* , which was captured shallowest, is known to feed largely on benthic crustaceans (Gelsleichter et al., 1999), while *Merluccius albidus*, *Hexanchus nakamurai*, *S. cubensis*, and *Centrophorus* spp., which are found deeper, feed on more pelagic prey (teleosts and squid) (Compagno, 1984; Cohen et al., 1990; Monzini, 2006; Ebert et al., 2009). Furthermore, some deep-sea fishes are known to perform considerable vertical movements throughout the water column (e.g. Shipley et al., 2017), which could facilitate benthic-pelagic coupling, thus transporting more isotopically depleted resources from the pelagic zone to greater depths on the slope (Trueman et al., 2014). The size-based enrichment of $\delta^{13}C$ and $\delta^{15}N$ exhibited by *S. cubensis* suggests prey switching throughout ontogeny, as larger individuals are able to ingest larger, and a more diverse suite of prey items, as in the Gulf of Mexico (Churchill et al., 2015).

Isotope data from the Exuma Sound also provide insights into the feeding dynamics of invertebrates. The high $\delta^{15}N$ values in isopods, for example *Bathynomus giganteus*, agree with observations from the Gulf of Mexico, and may attribute to a greater degree of scavenging compared to *Heterocarpus ensifer* (McAvoy et al., 2002; Churchill, 2015). High $\delta^{15}N$ in isopods may also be attributable to their broad depth range. This suggests individuals scavenge over broader regions of the slope, which increases the chance of encountering prey items exhibiting more enriched $\delta^{15}N$. Isopods can often be micropredators of larger fishes (Shipley et al., 2016), which would further explain high $\delta^{15}N$ values.

The large ranges, and depth patterns of both $\delta^{13}C$ and $\delta^{15}N$ indicate complexity within the Exuma Sound community. We also highlight how multiple factors, such as a changing mix of production sources, and changing community composition may directly affect $\delta^{13}C$ of deep-sea fauna. Future work should therefore focus on defining energy specific energy sources underpinning deep-sea communities, as well as examining clear predator-prey relationships across species. Finally, examining similar systems at other locales is suggested if the ecological significance and energy sources supporting these communities are to be better understood.

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7. Tables and Figures

Table 1 – Species, number of samples (*n*), mean $\delta^{15}N$, $\delta^{13}C$ and C:N **(**± SD) gathered from the Exuma Sound deep-sea slope community.

Species	Common Name	*n*	Capture Depth (m)	$\delta^{15}N$ (± SD)	$\delta^{13}C$ (± SD)	C:N (± SD)
Elasmobranchs						
Squalus cubensis	Cuban dogfish	22	462 - 727	9.98 (0.71)	-14.08 (0.70)	2.82 (0.08)
Centrophorus spp.	Gulper shark	9	731 – 818	10.62 (0.24)	-16.09 (0.24)	2.77 (0.12)
Mustelus canis-insularis	Smooth dogfish	6	462 – 655	9.10 (0.32)	-11.83 (0.91)	2.82 (0.10)
Hexanchus nakamurai	Bigeye sixgill shark	4	534 – 641	11.23 (0.05)	-13.80 (0.60)	2.89 (0.28)
Heptranchias perlo	Sharpnose sevengill shark	2	607 – 656	12.77 (0.56)	-16.49 (0.51)	2.86 (0.10)
Scyliorhinus meadi	Blotched catshark	1	602	8.03	-14.05	2.76
Other Fish and Eels						
Synaphobranchus affinis	Grey cutthroat eel	2	923 – 978	11.24 (0.59)	-15.42 (0.39)	3.15 (0.03)
Sebastes oculatus	Patagonian redfish	1	559	11.87	-14.42	2.86
Merluccius albidus	Offshore hake	1	731	13.93	-15.69	2.96
Polymixia nobilis	Stout beardfish	1	606	11.6	-13.6	2.94
Rhomboplites aurorubens	Vermillion snapper	1	461	10.07	-13.15	2.97
Conger sp.	Conger eel	1	748	12.05	-13.93	2.89
Nemichthys scolopaceus	Slender snipe eel	1	-	8.95	-16.19	2.97
Invertebrates						
Bathynomus giganteus	Giant isopod	10	656 - 912	12.57 (0.59)	-15.04 (0.51)	3.06 (0.17)
Booralana tricarinata	Small isopod	8	656	12.52 (0.92)	-15.68 (1.96)	3.16 (0.09)
Heterocarpus ensifer	Armed Nylon Shrimp	8	600 - 774	8.30 (0.71)	-14.23 (1.68)	2.85 (0.08)

Fig 1. Isotope bi-plot highlighting mean $\delta^{13}C$ and $\delta^{15}N$ (± SD) from the Exuma Sound fish (black squares) and invertebrate (open circles) community.

Fig 2. Deep-water species sampled from the Exuma Sound island slope community: a) *Squalus cubensis* (photo by: Brendan Talwar); b) *Heterocarpus ensifer*; c) *Centrophorus* spp.; d) *Bathynomus giganteus*.

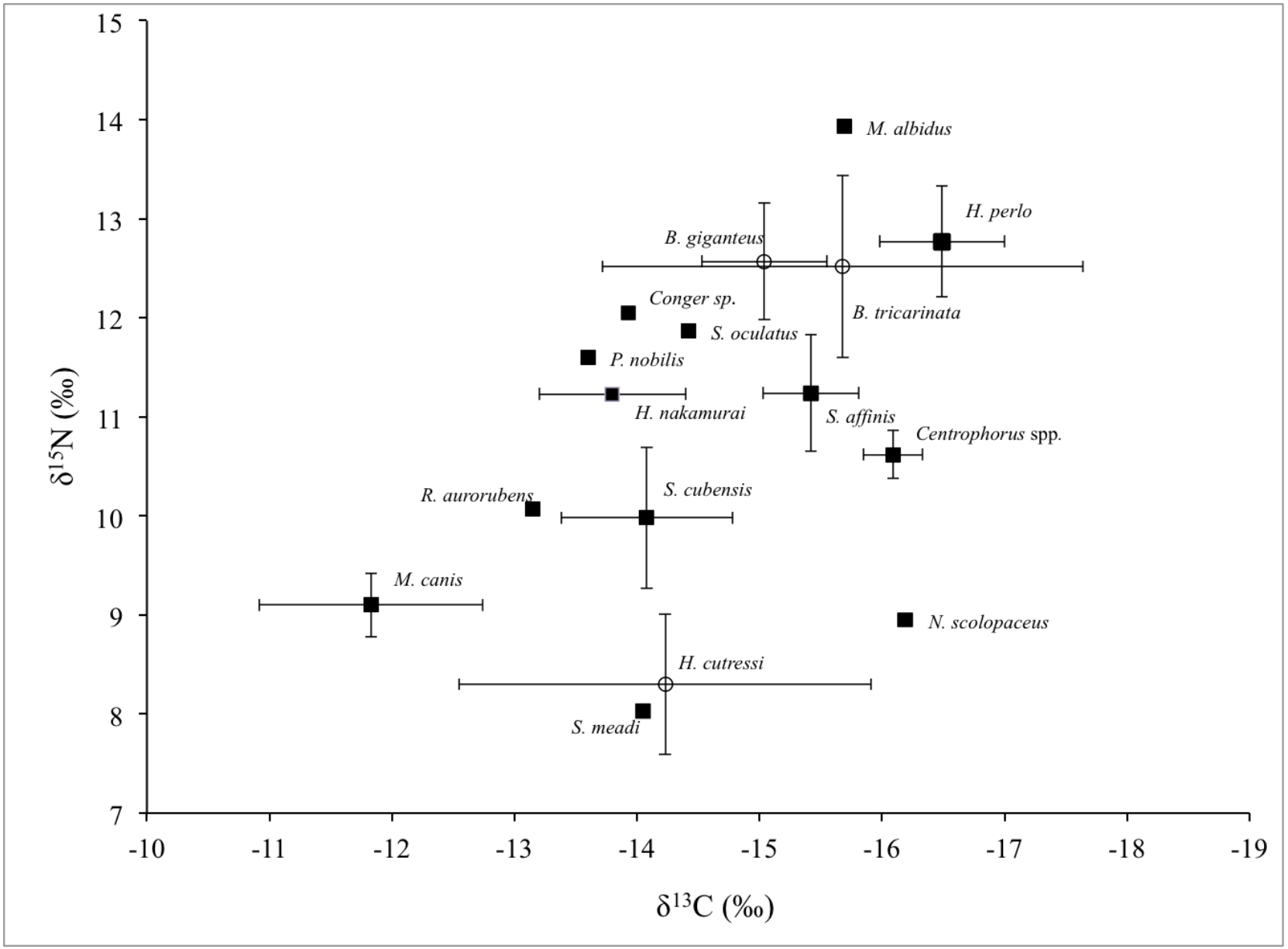

Figure 1

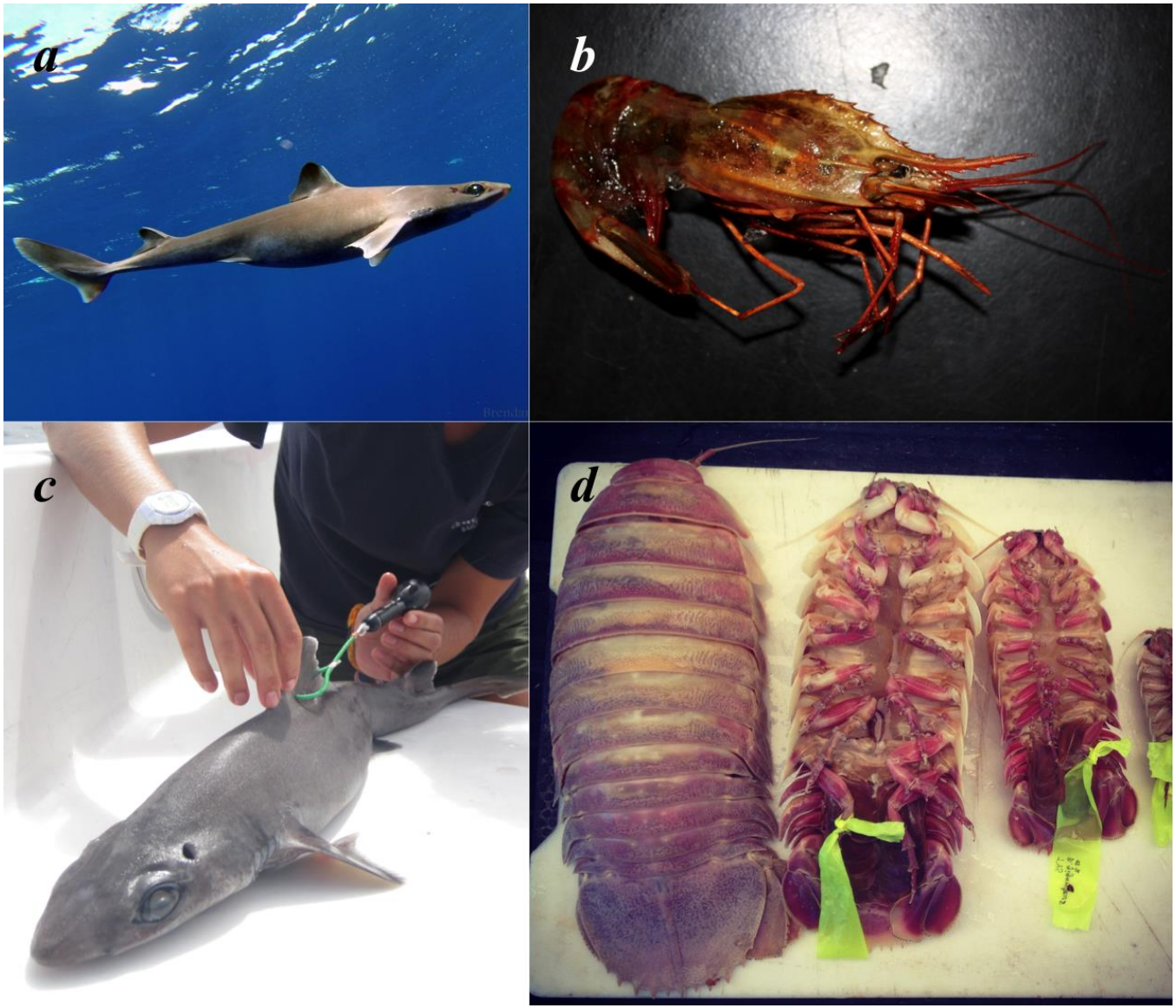

Figure 2